

Photosynthetically active radiation use efficiency of *Dactylis glomerata* and *Schedonorus phoenix* along a hardwood tree-induced light gradient

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Abstract Photosynthetically active radiation use efficiency (PARUE) of orchardgrass (*Dactylis glomerata* L.) and tall fescue (*Schedonorus phoenix* (Scop.) Holub) was determined. Leaf mass was harvested for canopies at different shade levels when each reached 20 cm height with 5 cm residue for regrowth to simulate grazing. Total incident PAR at each site was summed for the growth period (S-PAR). Values for PARUE were calculated from dried leaf mass divided by S-PAR. The more highly shaded plants reached 20 cm at lower S-PAR. While overall leaf mass decreased linearly with shade induced decreases in S-PAR, PARUE increased exponentially. The coefficients for the equations representing this exponential increase vary for forage species and may represent a useful index for characterizing forage response to silvopastoral systems.

Keywords Cloudiness · Forage · Growth · Shade · Solar angle

Introduction

A primary goal of agriculture and forestry is to harvest solar radiation using biological systems to

produce food and fiber. Silvopastoral systems are designed to simultaneously grow understory forages for livestock production along with trees for wood or other useful products. The economic success of silvopastoral systems requires proper management for capture and partitioning of solar radiation. Perhaps the most critical requirement is that well-adapted forage species are used as understory crops (Lee 1991; Devkota et al. 1998). In temperate regions an example of such an adapted species is orchardgrass (*Dactylis glomerata* L.). Tree shade changes light intensity and quality depending on tree species, seasons of year, time of day, and cloud cover. Light quantity and associated quality induces various morphological adaptations in understory plants such as leaf elongation, reduced specific leaf weight, and altered rates of tiller production (Devkota and Kemp 1999; Monaco and Briske 2000; Belesky 2005).

Determining radiation use efficiency (RUE) of crops can provide an insight into how well a given production system is functioning and how management might be modified for production improvements (Sinclair and Muchow 1999). For example, some newer cultivars of annual crops have higher RUE than older, lower-yielding ones (Tollenaar and Aguilera 1992; Calderini et al. 1997). In cereals, RUE decreases after anthesis (Campbell et al. 2001; Lindquist et al. 2005). In a corn (*Zea mays* L.)—bean (*Phaseolus* spp.) intercropping compared with monocultures, corn alone had the highest instantaneous RUE but the intercropping system had the greatest overall seasonal

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RUE (Tsubo et al. 2001). Nitrogen fertilization also affects RUE (Sinclair and Shiraiwa 1993; Hall et al. 1995).

Radiation intensity has an impact on RUE. In the case where radiation incident upon forages has been attenuated by trees, the issue of how vegetation responds to decreased radiation is complicated by the enrichment of far-red relative to red spectrum. Smith (1981), in his summary of plant adaptation to shade, generalized that shade avoiders (most crops fit this category) grow smaller leaves and more stem in response to a decrease in the red/far-red ratio but grow less stem and more leaf in response to a decrease in photosynthetically active radiation (PAR) only. Shade tolerators, however, have little change in morphology in response to changes in red/far-red ratio and merely increase RUE in response to reduced PAR. It is doubtful that many species fit exclusively into one category but represent a continuum of responses. For example, rice (*Oryza sativa* L.) had a 57% increase in RUE in response to 72% shade, and sunflower (*Helianthus annuus* L.) had a 236% increase in RUE in response to 75% shade, while both would be considered shade avoiders (Horie and Sakuratani 1985; Stirling et al. 1990).

Perennial forages function in a much different manner than annual crops, so RUE need to be evaluated somewhat differently. Forage grasses do not partition a large amount of their photosynthate into seed production because their strategy is to perenniate by producing vegetative propagules, helping the plants survive episodic defoliation. The primary structure of interest to pastoral agriculture is leaves. Faurie et al. (1996) found a negative correlation between PAR capture by mixed grass-legume swards and RUE. This suggests that PAR use efficiency (PARUE) of forages in moderately shaded (reduced PAR) silvopastures should be higher than in open pastures.

Silvopastures may improve total solar radiation harvesting compared to open pasture. However, there is much research needed to develop a reliable understanding of how to manage hardwood silvopastures in the Midwest and Eastern USA (Garrett et al. 2004).

Our primary objective was to test the hypothesis that the PARUE of the C₃ grasses orchardgrass and tall fescue (*Schedonorus phoenix* (Scop.) Holub) measured for leaf mass production to support rotational grazing, increases under tree shade in

silvopasture systems compared to open pasture. We also examined whether PARUE and simple yield of dried leaf mass (LM) resulting from differing shade levels within silvopasture systems was dependant on time within the growing season defined as day of year (DOY) or time between harvests (*N*-days). The analysis was for two experiments, one with orchardgrass in 2001 and 2002 and the other with tall fescue in 2004.

Materials and methods

The experiment site was in southern West Virginia, USA (81° 7' W, 37° 45' N, 760 m elev.) in an area that averages 1.1 m of uniformly distributed precipitation annually. The research was done adjacent to and within edges of a 30 × 400 m group selection clear-cut (a patch cleared within an otherwise undisturbed forest region) made 4 years prior to initiation of the experiment. The clear-cut was made within a second growth hardwood forest (mixed *Quercus* spp.). The long axis of the clearing was oriented east-west and the width was such that the region adjacent to and within the north edge forest received no shading from trees on the southern edge throughout the growing season. The remaining forested area had achieved a closed canopy height of about 25 m. Mowing the site during the 4 year preceding this experiment facilitated development of a low canopy of mixed forbs, grasses, and bare patches within the clearing and forest edge. Vegetation became increasingly sparse with distance into the forest relative to the open sites.

The deciduous forest began leaf extension early to mid May (DOY 130) and began shedding leaves in mid October (DOY 290). Pasture grasses began sustained growth around 10 April (DOY 100) and this continues until 30 days after tree leaf-fall, but these dates can be highly variable.

We used orchardgrass, (cv. 'Benchmark'), and tall fescue, (cv. 'Jesup' and 'MaxQ'), for these experiments. Multi-plant canopies were established in 2.5 L containers containing a mixture of four parts soil (Lily, fine-loamy, siliceous, semi-active, mesic, Typic Hapludult) (Soil Survey Staff 2004) and three parts sand sown with 100 seeds per pot. During establishment, plants were allowed to develop uniform full canopies of about 0.02 m² in a glass house.

Container-grown plants eliminate or minimize site and soil related effects on establishment, growth, and nutrient availability (Monaco and Briske 2000). Bottoms were removed from the containers before placing in the ground, while sides of containers remained intact.

During 2001 and 2002, orchardgrass pots were placed into each of four shade treatments. An open (O) treatment in the clearing with no solar shading by trees, a wooded (W) treatment 25 m within the forest that received no direct beam solar radiation except from sun flecks, and two intermediate north edge treatments under trees 3 and 6 m, respectively, (N3 and N6) from the forest edge. These shade treatments were analyzed twice. The first time a set of containers was planted early May, on DOY 127, 2001 when the trees were just starting bud break to analyze the response of spring planted grass. A second set was planted on DOY 242 in late August, 2001 and allowed to vernalize in the field to evaluate the response of autumn planted grass growing the following season.

The containers with tall fescue were placed within the wooded edges on the north and south sides on DOY 120, 2004. Sufficient containers were established to allow for three harvests at each shade level with three replications at each harvest. On the north edge the containers received differing amounts of direct and diffuse radiation while within the south edge they received similar amounts of direct beam radiation but differing amounts of diffuse radiation. Containers were placed in the open (O) clearing where they received no shading from trees and 2, 4, and 6 m into the forest from the north and south edge respectively of each tree line (N2, N4, N6, and S2, S4, S6).

Baseline data on plant size were collected from nine replicates immediately prior to field placement for another study (Belesky 2005), at which time all plants were clipped to a 5-cm residual plant height. Three replicate containers were randomly collected and destructively sampled each time mean plant height reached 20 cm. Remaining plants were clipped to 5 cm and allowed to regrow to 20 cm, the time (*N*-days) differing between shading levels. Plants (grasses and forbs) surrounding pots at each micro-site were clipped to 5 cm height each time experimental plants were clipped to retain a uniform fetch boundary.

To determine PAR for each of the light treatment zones, a system of LI-COR LI-191-SB 1-m line

quantum sensors (LI-COR Lincoln, NE) was installed at intervals during the growing season with data recorded using a Campbell Scientific 21X data logger (Campbell Scientific Inc., Logan, UT). One sensor was placed at the O site, and two at each of the other sites. Data collection was timed to capture values during tree leaf extension (DOY 133–143); early (DOY 150–164), mid (DOY 218–228), and late summer (DOY 258–264); and post leaf drop (DOY 303–310). Using these data, PAR values were extrapolated for all periods using PAR data from an automated weather station in the clearing equipped with a LI-190SZ quantum sensor. Maximum potential PAR above the tree canopy level throughout the year (Max) was calculated for the specific longitude and latitude using WinSCANOPY software (Instruments Regent Inc., Quebec, Canada).

The parameter PARUE was defined as the 15 cm of dried leaf mass (LM) produced between the time when the grass was clipped to 5 cm height and the grass grew to 20 cm divided by the summed daily PAR (S-PAR) received during that time. For the first harvest of 2002 S-PAR was from DOY 100 (10 April), which approximated when forages began sustained spring growth across treatments.

Relationships between both LM and PARUE as a function of DOY, *N*-days, and S-PAR were analyzed using regression analysis. The DOY was simply used as a linear scale to assess if LM and PARUE changed as the growing season progressed.

Results

At this location, oaks generally began leaf extension around DOY 120. By DOY 130 tree canopy approached half of full leaf extension and leaves were fully extended by DOY 150 at which time PAR at shaded sites no longer decreased relative to that at O (Fig. 1a, b). By DOY 200 solar angle had decreased such that a substantial increase in PAR occurred at sites within the north edge since direct beam radiation passed increasingly under the canopies of the edge trees. Leaves began falling in early October 2001 (DOY 280) and PAR at site W for pots placed for the 2002 harvest began to increase. By DOY 305 leaf fall was complete and site W PAR increased to about 60% of that at O (Fig. 1a). During periods where trees were leafless, sites N3 and N6

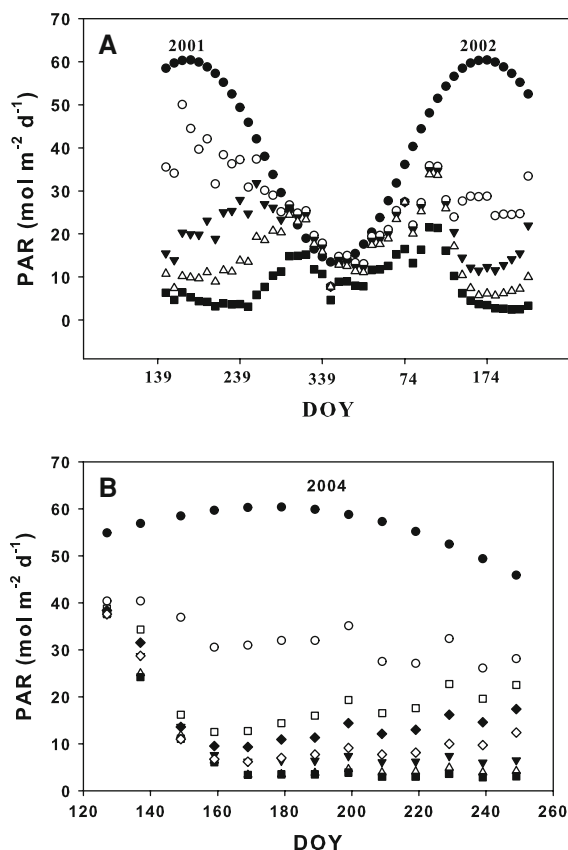


Fig. 1 Seasonal PAR for (a) orchardgrass in 2001 and 2002 and (b) tall fescue in 2004. The x-axis represents day of year (DOY). For 1a, symbols indicate data points modeled by WinSCANOPY (●), open (○), 3 m within northern forest edge (▼), 6 m within northern forest edge (Δ), 25 m within northern forest edge (■). In the text these treatments are referred to as Max, O, N3, N6, and W, respectively. For 1b, symbols indicate data points modeled by WinSCANOPY (●), open (○), 2 m within northern forest edge (□), 4 m within northern forest edge (◆), 6 m within northern forest edge (◇), 2 m within southern forest edge (▼), 4 m within southern forest edge (Δ), and 6 m within southern forest edge (■). In the text these treatments are referred to as Max, O, N2, N4, N6, S2, S4, and S6, respectively

received PAR levels similar to O. During 2004 the same pattern in PAR reception was evident at the north edge, however, at the south edge PAR for all sites remained constant relative to site O throughout the summer (Fig. 1b).

Actual PAR was modified by cloudiness relative to maximum potential PAR at site O (Fig. 1a, b). At the other sites PAR impinging on the forage canopy was limited by both cloudiness and to different degrees, trees. Sites on the north edge had PAR similar to site O in the spring prior to tree leaf extension and each of

the two edge sites approached O at different times in late summer of 2001 as solar angle decreased. Because of shading from tree boles and branches, site W never converged with site O PAR. Forages growing in deciduous silvopastures experience fluctuating PAR caused by the net effects of solar angle, cloudiness, and location relative to trees. There were variations in PAR from year to year as a result of variability in large scale climate patterns (Tables 1, 2). The late spring-early summer PAR at site O was 67% and 45% of Max for 2001 and 2002, respectively (Table 1), which resulted in relative differences in PAR at the other sites. For 2004 PAR was 55% of Max (Table 2).

Leaf mass at each harvest was a measure of forage produced as the canopy grew from 5 to 20 cm and there was a significant trend of greater LM at higher PAR sites (giving high S-PAR) (Fig. 2a, b). Plants in lower PAR environments elongated more rapidly and produced less LM at 20 cm. The spring planted orchardgrass retained juvenile characteristics (many small tillers) throughout 2001 and produced much more LM at any given PAR level than when autumn-planted. The autumn-planted plants, which vernalized over winter, produced fewer but much larger tillers and put more photosynthate into root mass (Belesky 2005). Tall fescue in 2004, even though spring planted, began producing fewer but larger tillers during the summer at high PAR levels. There was a significant decrease in LM with successive harvests (Table 3) as the summer progressed (later DOY) for orchardgrass in 2002 and for tall fescue in 2004.

Table 1 Actual and relative PAR received by orchardgrass averaged for a 7-week period bracketing summer solstice where O designates open, N3 and N6 are 3 and 6 m from the north forest edge, respectively, and Max is potential PAR had there been no cloudiness

Measurement site	O	N3	N6	W	Max
<i>PAR (mol d⁻¹)</i>					
2001	39.7	18.7	9.7	4.9	59.3
2002	26.8	10.7	6.9	3.7	59.3
<i>% of Open (100-Shade)</i>					
2001	100	47	24	12	
2002	100	40	26	14	
<i>% of Max</i>					
2001	67	32	16	8	
2002	45	18	12	6	

Table 2 Actual and relative PAR received by tall fescue averaged for a 7-week period bracketing summer solstice where O designates open, N and S north and south forest edges, respectively, and 6, 4, 2 the number of meters from the forest edge, and Max is potential PAR had there been no cloudiness

Measurement	O	N2	N4	N6	S2	S4	S6	Max
site								
PAR (mol d^{-1})								
2004	32.6	14.6	11.1	7.3	7.5	5.4	4.9	59.3
% of Open (100-shade)								
2004	100	45	34	22	23	17	15	
% of Max								
2004	55	25	19	12	13	9	8	

Table 3 Regression statistics for the equation $y = a \cdot x + b$ where S-PAR is the sum of PAR for the harvest growth period, LM is leaf mass, DOY is day of year, N -days is the number of days in the harvest growth period, and PARUE is PAR use efficiency

Year	Y	X	A	B	r^2	P
2002	LM	DOY	-0.38	142	0.30	<0.05
2004	LM	DOY	-0.07	199	0.27	<0.05
2001	LM	N -days	1.30	68	0.19	0.053
2002	LM	N -days	1.11	17	0.24	0.064
2002	PARUE	N -days	-0.0080	0.55	0.64	<0.01

Orchardgrass was grown in 2001 and 2002 while tall fescue was grown in 2004

There was a numerical trend ($P = 0.053$ and 0.064 for 2001 and 2002, respectively) of increasing LM with increasing N -days for orchardgrass (Table 3). This was consistent with higher LM at higher PAR where elongation was not as rapid as at low PAR. The trend was not evident for tall fescue in 2004.

There was no significant relationship between PARUE and harvest DOY for any year. There was a negative relationship between PARUE and N -days for orchardgrass in 2002 that was highly significant; however, the relationship was not significant for orchardgrass in 2001 or tall fescue in 2004.

For all 3 years PARUE decreased exponentially as S-PAR increased (Fig. 3a, b). Orchardgrass had consistently higher PARUE in 2001 compared to 2002 in spite of overall higher PAR in 2001. This was because of the larger leaf mass of non-vernalized plants which tend to allocate more photosynthate to leaves to consolidate their “place” to a particular site.

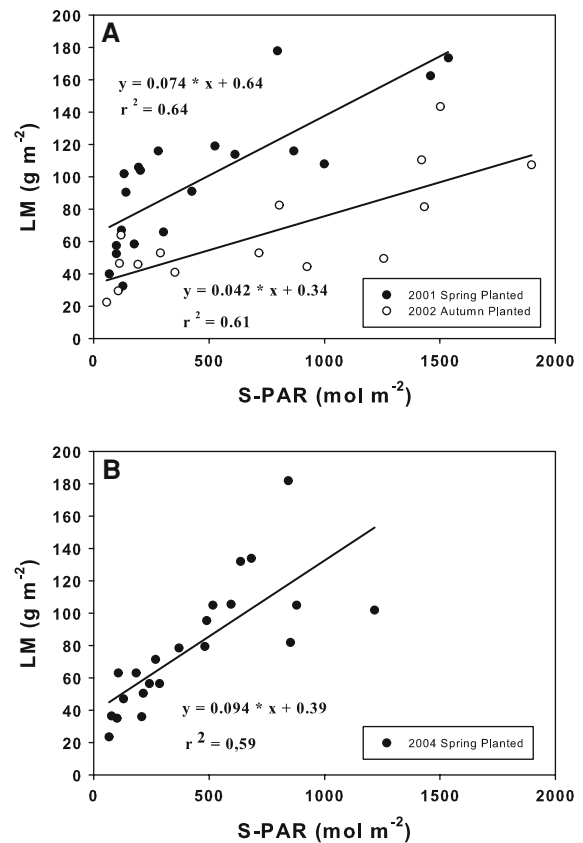


Fig. 2 Leaf mass (LM) as a function of S-PAR during the period of elongation from 5 to 20 cm for (a) orchardgrass in 2001 and 2002 and (b) tall fescue in 2004. Each point represents a harvest from differing PAR levels across plots and light gradients

Discussion

We explored the relationship between forage production and deciduous-tree mediated PAR levels in such a manner that PAR effects were imposed with little interaction between tree and grass roots and minimal influence from microbial communities or nutrient availability. Treatments were situated in woodlot edges facing north or south, with potential PAR levels at each shaded site relatively constant compared to the O site throughout most of any given day. The exception is very early and late in the day when trees cast much more shadow than at midday. However, PAR was not high at these times so the influence on total daily accumulated PAR was small.

There are several mechanisms by which forage grasses adapt to low PAR. They adapt when growing

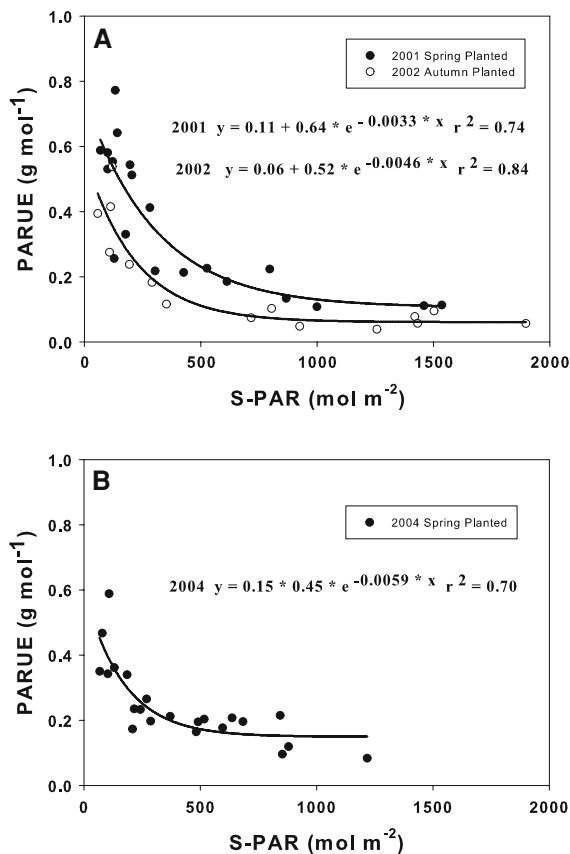


Fig. 3 PARUE as a function of S-PAR received along the light gradient for grass growth during the period of elongation between 5 and 20 cm. Each point represents a different harvest date-site combination for (a) orchardgrass in 2001 and 2002 and (b) tall fescue in 2004

in shade so their photosynthetic rate is higher at low PAR than for full sun-adapted plants at low PAR (Peri et al. 2002), leaves elongate using less structural fiber per unit length, and less photosynthate is allocated to roots and crown, but more is directed toward leaf production. Forage grasses might sustain some level of leaf elongation and production as a response to shading, but nutritive value measured in available herbage energy could be compromised (Belesky et al. 2006; Buergler et al. 2006). Energy expressed as structural fiber or readily available non-structural carbohydrates is less in shade grown plants than those grown in full sunlight. Since available herbage energy very often is a limiting factor in forage-based livestock production systems, Belesky et al. (2006) and Neel et al. (2008) found that silvopastures might maintain productivity (forage mass) yet not satisfy grazing ruminant energy

requirements. Many of these adaptations are associated with changes in the red/far-red ratio that occurs along with changes in PAR (Wherley et al. 2005).

In other research forage production has consistently correlated linearly with increasing S-PAR. The slope of the linear relationship of biomass production as a function of intercepted radiation has defined RUE (Sinclair and Muchow 1999). In this study, the PARUE to S-PAR relationship was also linear even though harvest date was not determined by time but rather by leaf-elongation. However, the timing of daily shade has resulted in increased forage production if factors such as high temperature stress are prevented. Buergler et al. (2005) observed slight increases in forage production in black walnut (*Juglans nigra* L.) and honey locust (*Gleditsia triacanthos* L.) silvopastures when forages received full sun most of the morning but mottled shade midday and afternoon. Garrett and Kurtz (1983) also found forages shaded by black walnut had greater yields than when grown in open fields.

Under controlled environmental conditions, Faurie et al. (1996) found that perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) RUE decreased exponentially as the mean amount of PAR capture per leaf area increased. In this forest-field interface study the same functional relationship was found for orchardgrass and tall fescue. This presented an opportunity to examine forage response to decreasing S-PAR in a way other than as the linear decrease in LM.

The regression parameters for the exponential relationship between PARUE and S-PAR found in this study and similarly by Faurie et al. (1996) were analyzed separately to interpret how they were related to plant response. The parameter y_0 was a baseline characterized by PARUE at high S-PAR levels and the region within which the curve was nearly horizontal suggested minimal adaptation to increasing shade (Fig. 4a). The coefficient “a” was positively related to the rate of increase in PARUE as S-PAR levels decrease (Fig. 4b). The coefficient “b” was negatively related to how much S-PAR needed to decrease before PARUE began increasing (Fig. 4c) which suggested the shade level at which plant adaptation began.

In future experiments, comparisons of these parameters may provide a useful analysis for comparing forage species in differing silvopastures. In this experiment the juvenile 2001 orchardgrass had the

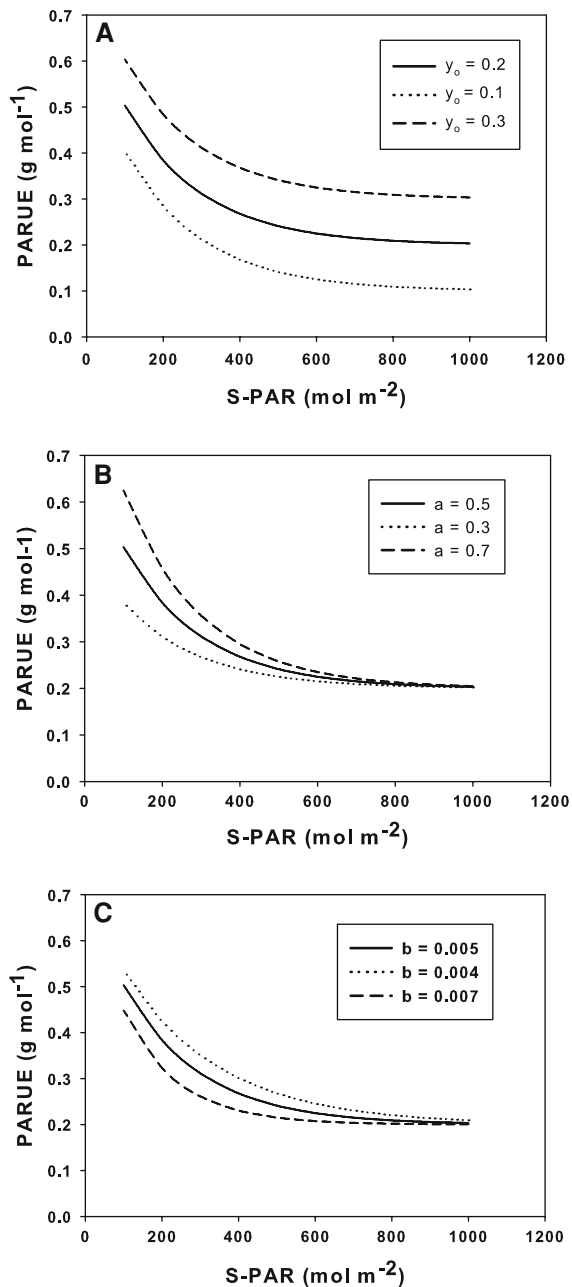


Fig. 4 The relationship between PARUE as a function of S-PAR using an equation of the form $y = y_0 + a * e^{-b * x}$ and reference values of $y_0 = 0.2$, $a = 0.5$, and $b = 0.005$ compared to (a) $y_0 = 0.1$ and 0.3 , (b) $a = 0.3$ and 0.7 , and (c) $b = 0.004$ and 0.007

highest “a” value and the lowest “b” value since it yielded best at the more shaded sites compared to mature orchardgrass or tall fescue. Tall fescue had the lowest “a” and the highest “b” indicating it was not adapted as well to shade, however, it had the highest y_0

suggesting it was best suited for sunny sites. In screening for potential useful C_3 silvopasture forage species or cultivars, a high “a” and a low “b” are desirable. There was no consistent correlation between PARUE and DOY or N -days suggesting that at least in moderately high elevations like much of Appalachia, the relationship between PARUE and S-PAR is seasonally stable. Different indices may be applicable to C_4 species.

These results were from a site with a uniform tree canopy. There is some evidence that higher PARUE may be realized in silvopastures with trees planted in north-south rows. Buergler et al. (2005) found no statistical difference in forage yield between a high shade treatment and an unshaded treatment under black walnut and honey locust in north-south rows even though there was a 67% decrease in total daily PAR. Feldhake et al. (2008) similarly found in 2 out of 3 years no decrease in forage yield under black locust (*Robinia pseudoacacia* L.) rows compared to alley centers even though sunny, mid-day PAR was attenuated by 80% under tree rows.

Conclusions

While LM increased linearly with S-PAR, PARUE values decayed exponentially. The coefficients for the exponential decay showed promise for quantifying forage PARUE at high PAR levels (y_0), the minimal amount of PAR reduction imposed that initiates plant adaption (b), and the rate of adaption at increasingly low PAR levels (a).

Most improved tall fescue and orchardgrass cultivars have been selected for productivity in open field sites with high PAR. Production and persistence in silvopasture might benefit from breeding and selection of shade-adapted forage species with improved non-structural carbohydrate production to help maintain digestible energy levels. Tailoring forage plant resources to silvopasture system needs, for instance plants with high light use efficiency and low light compensation point (Van Huylenbroeck et al. 1999), promises to improve productivity and utility of silvopastoral systems. Evaluation of different forage species, cultivars, and tree planting configurations for silvopastures using PARUE as a function of S-PAR in the form $y = y_0 + a * e^{-b * x}$ might provide insights on systems function and management.

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